A Revision of Agrostis billardierei R. Br. (Poaceae)

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Abstract

Observations of growth habit and habitats and statistical analysis of detailed morphological measurements on specimens of *Agrostis billardierei* R. Br. and some closely related taxa has resulted in a re-evaluation of the rank and status of some of them. New combinations are made for *Agrostis billardierei* var. *robusta* Vickery, *A. billardierei* var. *collicola* D. Morris, *A. billardierei* var. *filifolia* Vickery and *A. aemula* var. *setifolia* Vickery. The new names for these taxa are *A. robusta*, *A. collicola*, *A. punicea* var. *filifolia* and *A. punicea* var. *punicea* respectively. *Agrostis billardierei* var. *tenuiseta* D. Morris is confirmed as a good taxon.

Introduction

As a result of recent extensive surveys and collections of *Agrostis* in Western Victoria by the senior author, the status of some published taxa was in obvious need of reassessment. In particular, the morphological and ecological relationships between *A. billardierei* var. *filifolia* Vickery and *A. aemula* var. *setifolia* Vickery appeared to be a lot closer than implied by their taxonomic status. In contrast, a number of the recognised varieties of *A. billardierei* R. Br. appeared to be more distinct than their status would indicate. For example, James and Brown (2000) found highly significant differences in both morphological assessment and DNA analysis, when comparing single populations of *A. billardierei* var. *robusta* and *A. billardierei* var. *filfiolia*.

Vickery (1941) carried out the last major revision of the Australian species of *Agrostis*. Working with a limited number of specimens, she recognised three varieties of *A. billardierei*, viz. *A. billardierei* var. *billardierei*, from coastal New South Wales, Victoria, Tasmania and South Australia (20 specimens recorded), *A. billardierei* var. *filifolia*, from inland Victoria and Tasmania (2 specimens recorded) and *A. billardierei* var. *tobusta* Vickery, also from inland Victoria and Tasmania (2 specimens recorded). Since 1941, many other specimens of *A. billardierei* var. *filifolia* (2 specimens recorded) and Jessop and Toelken (1986) added *A. billardierei* var. *tobusta* (2 specimens recorded) and Jessop and Toelken (1986) added *A. billardierei* var. *tobusta* (2 specimens recorded) to the South Australia flora. Morris (1990) recognised additional varieties of *A. billardierei* from Tasmania, viz. *A. billardierei* var. *collicola* D. Morris (2 specimens recorded) and *A. billardierei* var. *billardierei* var. *collicola* D. Morris (2 specimens recorded) and *A. billardierei* var. *billardierei* var. *collicola* D. Morris (2 specimens recorded) and *A. billardierei* var. *billardierei* var. *collicola* D. Morris (2 specimens recorded).

Agrostis billardierei var. robusta was separated from var. billardierei on the basis of its taller, rather rigid habit, non-littoral habitat, narrow, inrolled, acuminate leaves, more conspicuously scaberulous lemmas and smooth to scaberulous-sided glumes with very scabrous keels (Vickery 1941). Agrostis billardierei var. filifolia was separated from the typical variety on the basis of its more slender and rather taller habit, non-littoral habitat, very narrow, almost filiform leaves, rather few-flowered and more capillary panicles, long anthers and smooth-sided glumes (Vickery 1941). Agrostis billardierei on the basis of their slender, straight, sub-terminal awns (or awns sometimes absent in the case of the latter) and from each other on the basis of their differing habitat and stature (the former growing in non-littoral highlands and being smaller with few spikelets) (Morris 1990).

Vickery (1941) also described *Agrostis aemula* var. *setifolia* based on 3 specimens from Tasmania. Walsh and Entwisle (1994) recorded this taxon for Victoria. *Agrostis aemula* var. *setifolia* was separated from var. *aemula* on the basis of its very narrow, setaccous or sub-filiform leaves, more lax panicle, longer lemmas, awn insertion much below the middle, and long anthers (Vickery 1941). Vickery also noted: "It shows a very close superficial resemblance to *A. billardierei* var. *filifolia*, but differs in the very pubescent lemma."

Taxonomic keys appearing in current Floras (e.g. Jessop & Toelken 1986, Simon 1993, Walsh & Entwisle 1994, Curtis & Morris 1994) largely follow Vickery's key (Vickery 1941).

Using morphological characterisation, this paper presents a statistical assessment of the relationships between these taxa and an enhanced description of each taxon. In addition, geographic distribution and environmental niches are noted.

Methods

MORPHOLOGY

Field collections of *Agrostis* specimens were made throughout southern Victoria over the growing seasons of 1993/94 to 1998/99 and measurement of a range of morphological characters were made (Appendix 1) for each specimen. The majority of the collection sites were located in south-west Victoria but some specimens were collected from Gippsland (eastern Victoria). Additional collections were made of *A. billardierei* var. *tenuiseta* from the cast coast of Tasmania, where it is endemic. As *A. billardierei* var. *collicola* is confined to a few Tasmanian highland localities (Morris 1990) and fresh field collections were not readily available, measurements were made on the few extant herbarium collections.

Total height was measured from the base of the above ground plant parts to the highest part of the plant (almost always, the inflorescence) while basal tussock height was a more subjective measure of the height of the major leafy part of the tussock. Culm height was taken from the plant base to the base of the highest flag leaf. Basal leaf width measurements were of the widest non-senescent leaf and flag leaf and inflorescence measurements related to the largest inflorescence in each specimen. The width of conduplicate or involute leaves was measured without flattening these leaves out (in accord with published descriptions and keys). Leaf roll was assessed for the majority of green leaves. Inrolling, or conversely, flattening sometimes occurred where leaves had senesced, but these were not used for leaf width measurements. Where an inflorescence was not exserted from the leaf sheath, the length of the visible peduncle was recorded as zero. The height of the inflorescence was taken from the base of the flag leaf or from the lowest panicle whorl if exserted. Spikelet measurements were made under a binocular microscope (20× mag.) on one 'typical' spikelet selected from each specimen. Occasionally, where an anther was found to be missing, an anther from another spikelet of similar age and size on the same specimen was measured. Pedicel and spikelet colour was assessed as the degree of purpling (assumed to result from the accumulation of anthocyanin).

The lemma and palea of some specimens have apical nerve extensions or 'tecth' of considerable length (up to 1.5 mm and 1.2 mm respectively). All such projections are termed 'setac' here.

Specimens were also classed according to plant age. This criterion was assessed on the maturity of the measured inflorescence, and divided the specimens into 'immature' (only partly exserted and non-spreading with non-senesced spikelets), 'maturing' (becoming exserted and/or spread with non-senesced spikelets), 'mature' (fully spread with terminal spikelets senesced) and 'ripe' (most of paniele senesced).

Agrostis billardierei and A. aemula and their varieties, were determined with the use of Vickery's taxonomic key (Vickery 1941) and Morris' descriptions (Morris 1990). Only the published key characters and not the full set of measured characters were used for determination. Vickery's key character for growth habit was poorly specified (i.e. 'tall and robust' for *A. billardierei* var. *robusta* and 'slender' for *A. billardierei* var. *filifolia*) and was consequently excluded from consideration. The key character of habitat (i.e. littoral or non-littoral) was also excluded. On examination of the data set, it was found that the key maximum limit for spikelet length of *A. aemula* was often exceeded and so only the key minimum limit was used for determination. Where specimens did not meet all accepted key criteria for a particular taxa, they were listed as indeterminate.

STATISTICAL TREATMENT

A total of 243 specimens were subjected to statistical analysis. Morphological data for analysis were either quantitative (continuous variable) or qualitative (discrete variable). Thirty six characters were assessed (including 12 discrete variables) and a further 14 characters were derived as ratios (e.g. inflorescence height:width), percentages (e.g. basal tussock height as a percent of total plant height) or sums (e.g. lemma body + lemma setae = total lemma length) from these. Qualitative data were transformed to an ordinal scale and treated as quantitative for some analyses. Ordinal scales varied from 3 to 5 levels, with an average of 3.8 (Appendix 1).

A selected set of 33 characters was used for multivariate analysis, including 10 of the qualitative characters (Appendix 1). None of the derived characters were used. As multivariate analysis cannot easily handle missing data, characters with missing data (number of visible branches in lowest inflorescence whorl, pedicel colour and spikelet colour) were also excluded.

All statistics were performed using the GENSTAT 5 package (Release 3.1, Lawes Agricultural Trust, Rothamstead Experimental Station).

A Symmetric Matrix (SYMMETRICMATRIX) of associations for the selected data set (using euclidean or cityblock variate type; the former for continuous variables and the latter for discrete variables), was established by forming a Similarity Matrix (FSIMI-LARITY). This matrix was then subjected to Principle Coordinates Analysis (PCO) to assess natural groupings of the specimens and to check the validity of the current flora key determinations. Separate PCO analysis was carried out on i) the above data set without exclusions and ii) the same data set but excluding 'immature' and 'ripe' specimens.

Discriminant (DISCRIMINANT) analysis was undertaken on the selected data sets to estimate mis-determination rates for specimens and to assign indeterminate specimens to groups. Separate discriminant analysis was carried out on: i) the selected data set without exclusions; ii) the selected data set but excluding lemma surface characters (i.e. B, Rc, Rd); and iii) the selected data set but excluding the varieties of *A. aemula*. Correlation matrices of variates and discriminant scores enabled the identification of those variates (i.e. characters) that were most influential in separating groups (i.e. taxa).

A Reduced Similarity Matrix (REDUCE) was constructed on the total (determined and reassigned) specimen data set of selected characters, using the mean similarity between groups. Hierarchical Cluster Analysis (HCLUSTER) (using the furthest neighbour criterion) of the Reduced Similarity Matrix, provided an association of the taxa for the purpose of assessing specific and varietal status. Furthest neighbour linkage was used to maximise space-dilation and minimise overlap between groups.

Ranges, means and significant differences for all measured characters (Appendix 1) were assessed by using Analysis of Variance (ANOVA) and provided for: i) identification of diagnostic characters to separate particular taxa; and ii) an enhanced description of each taxon. Least significant differences (LSD) at the 5%, 1% and 0.1% level were used to test differences in means between any two taxa.

Additional ANOVA was performed for each separate taxon to test the effect of plant age on the measured characters. Although it is recognised that this analysis was of age classes that contained specimens from varying and often different populations, it can still provide some useful overall information for each taxon.

EXAMINATION OF HERBARIUM SPECIMENS

Approximately 280 herbarium specimens (including type specimens and 33 duplicates) from MEL, AD, HO, NSW, CANB, K. BM, WELT and CHR were examined to check conformity of: a) survey specimens to type specimens and b) other herbarium specimens to survey specimens. Measurements were not routinely undertaken on these specimens, but only for some characters where individuals required re-appraisal or confirmation of the determination. These data were not included in the statistical analysis.

HABITAT MEASUREMENTS

Observations were made of the habitats occupied by each taxon for the field collected specimens. Composite soil samples (0-10 cm depth) were taken from a selection of sites and analysed for moisture content, pH (1:5 soil:water) and electrical conductivity (1:5 soil:water). Sites were selected to include *Agrostis* populations with substantial plant numbers and to cover a wide geographic range in south-west Victoria. Fifteen plants at each of two populations of *A. billardierei* var. *robusta* and two populations of var. *filifolia* were tagged for observation of growth habit, flowering and longevity over the 1998/99 and 1999/00 growing seasons. In addition, the position of four tussocks of var. *billardierei* at each of two sites were noted in December 1997 or 1998 and observed again two years later. Flowering time during the 1998/99 season for this taxon was noted for a further four sites.

Results

TAXA DETERMINATION

Thirty eight specimens were classed as indeterminate on the basis of their failure to conform completely to Vickery's key (Vickery 1941). In the majority of cases, non-conformity was in only one character of the several provided by the key.

PCO analysis of the total data set, provided a clear separation of all taxa, except for *A. billardierei* var. *tenuiseta* and *A. billardierei* var. *collicola* which grouped with *A. billardierei* var. *billardierei* (Fig. 1). The first and second vectors of the coordination accounted for 41.0% of the variation detected, with the third, fourth and fifth vectors accounting for a further 22.5%. Restriction of PCO analysis to 'maturing' and 'mature' aged specimens (i.e. exclusion of 'immature' and 'ripe' panicles) made little difference to the outcome.

For the 205 determined specimens used in this study, mis-classification rate, as calculated through the discriminant analysis of data without exclusions, was zero and all taxa displayed clear separation (Fig. 2), including var. *collicola* from the type of *A. billardierei* by the first and third vectors (the latter not shown) and var. *tenuiseta* from the type by the second and third vectors. The majority of reassigned (previously indeterminate) specimens fitted well to the taxa assigned by the analysis.

Specimens conforming to *A. billardierei* (Vickery 1941, Morris 1990) numbered 152, with a further 20 indeterminate specimens being reassigned to var. *robusta* (12 specimens) or var. *filifolia* (8 specimens). Indetermination for var. *robusta* was caused by a less scabrid glume keel than expected or an excessive anther length, while in var. *filifolia*, insufficient anther length was the main criterion. In total, specimens of *A. billardierei* were determined as: 26 of var. *billardierei* (from 14 near-coastal and 2 inland sites); 75 of var. *robusta* (from 39 inland and 8 near-coastal sites); 52 of var. *filifolia* (from 17 inland sites): 11 of var. *tenuiseta* (from 4 coastal sites); and 8 of var. *collicola* (made up of 2, 2 and 4 specimens of var. *filifolia* from Meerlieu in central Gippsland were slightly separated from the rest of the taxon due to their smaller than average spikelets. This population was the only collection from Gippsland and may indicate a local form.

0.4

0.3

02

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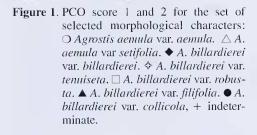
-0.1

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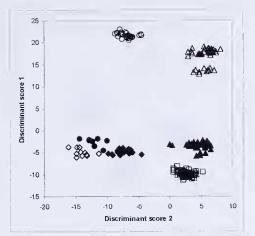
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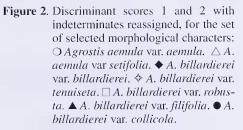
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PCO score 1



PCO score 2

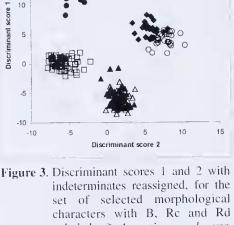




There were 53 specimens conforming to *A. aemula* (Vickery 1941). As *A. aemula* var. *aemula* appears to form intergrades with *A. avenacea* Gmel. (as noted by several authors e.g. Vickery 1941, Walsh & Entwisle 1994), only specimens with clear characteristics for *A. aemula* var. *aemula* (e.g. broad leaves and large spikelets) were used in this study to provide a comparison with *A. aemula* var. *setifolia*. A further 18 indeterminate specimens were reassigned to var. *aemula* (11 specimens) and var. *setifolia* (7 specimens). Indetermination was caused by excessive lemma length for var. *aemula*, and insufficient lemma length and anther length for var. *setifolia*. After reassignment, a total of 31 specimens of *A. aemula* var. *aemula* (from 16 inland sites) and 40 specimens of var. *setifolia* (from 17 inland and 1 near-coastal sites) were identified. Discriminant analysis separated var. *setifolia* into two, near but distinct, populations. On closer examination this was found to be due to the level of hairiness of the lemma back (i.e. level 3 or 4; see Appendix 1 for descriptions). There was no differentiation in the geographic range of these specimens.

The first and second vectors of the discriminant analysis accounted for 81.2% of the variation. The first vector was highly correlated with the characters for lemma surface (B, Rc, Rd at 0.97, -0.80 and -0.76 respectively) and therefore provided considerable separation of the current varieties *of A. aemula* and *A. billardierei*. Other characters with high correlation to the first vector were glume and awn length (Glb, Gub, Ab and Ac at 0.73, 0.67, 0.68 and 0.58 respectively), lemma setae length (Ls at 0.57) and glume margin ciliation (M at -0.55). The second vector was associated with leaf width and leaf roll (Llw, Lfw and Lr at -0.83, -0.74 and 0.80 respectively), awn attachment (Aa at -0.81), palea setae and body length (Ps and Pb at 0.72 and 0.54 respectively), density of lemma back scabridity (Rd at 0.58) and awn column length (Ac at 0.50).

Discriminant analysis of the data after exclusion of lemma surface characters (i.e. hairiness or scabridity; B, Rc and Rd) brought *A. aemula* var. *setifolia* and *A. billardierei* var. *filifolia* together into the same grouping (indicating that only lemma surface charac-



exluded: O Agrostis aemula var. aemula. $\triangle A$. aemula var setifolia. ♦ A. billardierei var. billardierei. ♦ A. billardierei var. tenniseta. 🗆 A. billardierei var. robusta. 🔺 A. billardierei var. filifolia. • A. billardierei var. collicola

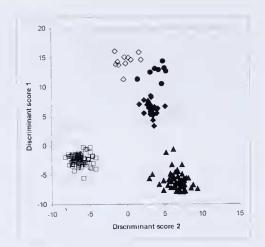


Figure 4. Discriminant scores 1 and 2 with indeterminates reassigned, for the set of selected morphological characters with the varietics of Agrostis var. billardierei. ♦ A. billardierei var. *tenuiseta*.
A. *billardierei* var. robusta. A. billardierei var. filifolia. • A. billardierei var. collicola

ter differentiates them) and resulted in a slight overlap of A. aeuula var. aeuula and A. billardierei var. billardierei in the first and second vectors (Fig. 3). Miscalculation rate was 4.4%, resulting from reassignment of four A. billardierei var. filifolia specimens to A. aemula var. setifolia and reassignment of five specimens from the latter to the former. There was no reassignment from A. aenula var. aenula to A. billardierei var. billardierei. The first and second vectors accounted for 85.4% of the variation. Separation by the first vector was largely influenced by awn attachment and length, palea setae length, leaf roll and width and anther length. The second vector was influenced by leaf roll, glume length, coarseness of lemma scabrids, glume margin ciliation, panicle stiffness and awn length.

Discriminant analysis of the varieties of A. billardierei alone, provided clear separation of all taxa (Fig. 4). Miscalculation rate was zero and the first and second vectors accounted for 80.4% of the variation. Separation by the first vector was mainly due to awn length and attachment, leaf roll and width, density of lemma scabrids and lemma and palea setae lengths while the second vector was influenced by coarseness of lemma scabrids, glume margin eiliation, anther length and paniele stiffness.

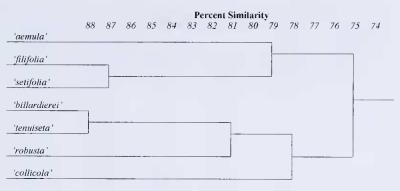
TAXA ASSOCIATION

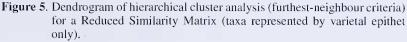
A dendrogram for the cluster analysis of the reduced similarity matrix is shown (Fig. 5). A. aemula var. aemula separates from A. billardierei var. billardierei at 75% similarity while A. aeuula var. setifolia, A. billardierei var. collicola and A. billardierei var. robusta separate from their type varieties at 79%, 78% and 81% respectively. Agrostis billardierei var. filifolia is elustered with A. aenula var. aenula rather than with A. billardierei var. billardierei and has 87% similarity to A. aeumla var. setifolia. A. billardierei var. tenuiseta has 88% similarity to A. billardierei var. billardierei.

20

15

10





KEY CHARACTERS

The results of ANOVA analysis based on currently recognised taxa are shown in Table 2. Except for inflorescence extension (Ie), inflorescence height to width ratio (Ih:Iw) and visible peduncle length (Ipd), significant differences were found for all measured characters at $P \le 0.001$.

Table 1 summarises significant differences for LSD at the 0.1%, 1% and 5% levels for a number of taxa comparisons. Although this analysis has identified numerous characters that are significantly different, most of these cannot be used as distinctive diagnostic characters for separating taxa because the range in their values overlap. However, a number of diagnostic or nearly distinct characters can be identified for each taxon.

Agrostis aemula and A. billardierei

Fifty four percent of the measured or derived characters were significantly different between *A. aemula* var. *aemula* and *A. billardierei* var. *billardierei* (forty percent being highly significant for LSD at 0.1%). Eighty five percent of these characters related to spikelet characteristics and included glume, lemma and awn size (all larger in *A. aemula*¹). *Agrostis aemula* also had longer setae points to its glumes and lemmas, smoother glume margins and more uneven glume lengths (the lower being slightly longer). Tussock height was shorter for *A. aemula*, leaf width was narrower and leaf length was shorter.

Although most character measurements overlap between these species, the generally narrower leaves, larger glumes and awns and the hairy lemmas of *A. aemula* var. *aemula* serve to distinguish it from *A. billardierei* var. *billardierei*. Although the mean inflorescence height to width ratio was the same for these species, it did not exceed a value of two for *A. billardierei* but was up to five for *A. aemula*.

Agrostis billardierei var. tenuiseta

Thirty six percent of characters separated this taxon from var. *billardierei* (twenty six percent for LSD at 0.1%). It was diagnostically separate by its short awns, which had a minute or absent column and a near terminal lemma attachment.

The leaves of this taxon tended to be more loosely inrolled (and therefore narrower), the flag leaves were shorter (some had withered tips), the spikelets less gaping and the

¹ It is recognised that forms of *A. aemula* var. *aemula* with similar or smaller spikelets than *A. billardierei* var. *billardierei* are currently recognised within the former taxon but were not examined as part of the current study.

Table 1.Summary of significant differences (*** = LSD at 0.1%, ** = LSD at 1%, * = LSD at 5%) between various comparisons of currently recognised taxa (represented by varietal epithet only).

Character		`billardierei` to `tenuiseta`		<i>`billardierei`</i> to <i>`robusta</i> '			ʻsetifolia' 'toʻfilifolia'
Hgt, cm			***				
Llh, cm	***		* * *	*	***		
Llhp, %	***		*	**	***		
Ch, cm			***				
Chp, %				*			
Lr (1-5)		***	***	***	***	***	
Llw, mm	***	***	***	***	***	***	
Lfw, mm	***	***	***	***	***	***	
	**	**	***		***	*	
Lfh, cm	· · · · ·	**					
Lig, mm			***	***	***	**	
Ie (1-4)							
Ipd, cm			**	*			
IIb (no.)			*		***	***	
Ih, cm		3/c 3/c	***				
Iw, cm			* * *				
Ih:Iw							

Ia (1-4) Ipc (1-5)				*	*		
Sa $(1-3)$			***		*	***	

Sc (1-5)		ate ate ate	alaata		*		
Sg (1-4)		***	**				
Glt, mm	***		***	**	*	***	
Glb, mm	***		***	***		***	
Gls, mm	***		*	***		**	
Glsp, %			***	***		*	
Gut, mm	***		***	**		***	
Gub, mm	***		***	***		***	
Gus. mm			*	***		**	
K (0-3)			***				
M (0-2)	***	***		***	***		
Glt:Gut	***		**		***		
	***				***	*	*
Lt, mm		**			***	***	
Lb, mm Ls, mm	***	***			**		**
Lsp, %	***	***	*		*		*
	***					***	***
B(0-4)	***		***	* * *	***	***	
Rc(0-3)	***	*	***	***	**	***	***
Rd (0-3)						* * *	
Pt, mm	*			***	***	***	
Pb, mm	*	*	*	***	***	***	
Ps, mm				**	***	***	
Psp, %				-le ste			
Re, mm	*				*		
At, mm	***	***	***	**	***		**
Ac, mm	***	***	***	***	***	*	**
Ab, mm	***	***	***		***	***	*
Abp. %	**	***	***	*		***	
Aa, mm	*	***	***		***	***	
Aap, %		***	***	**	***	***	
-	*				***	***	
A, mm	-1-						

Table 2. Means for morphological characters of currently recognised taxa (represented by varietal epithet only); values in the same row that share the same letter are not significantly different (assessed by LSD at 0.1% level).

	billardierei	tenuiseta	collicola	robusta	filifolia	setifolia	aemula	LSD
ontaractor	o man arer or					0		(0.1%)
Hgt, cm	49 b	44 b	14 a	48 b	44 b	41 b	45 b	15
Llh, cm	33 e	29 de	8 a	27 cde	19 bc	15 ab	20 bcd	9.6
Llhp, %	68 c	70 c	59 bc	55 bc	42 ab	38 a	45 ab	16
Ch, cm	24 bc	24 bc	7 a	28 c	19 bc	17 b	20 bc	9.5
Chp, %	48 <i>abc</i>	55 bc	49 <i>abc</i>	57 c	43 a	41 a	44 ab	12
Lr (1-5)	1.0 a	1.7 bc	2.1 c	4.8 e	3.9 d	3.9 d	1.2 <i>ab</i>	0.61
Llw, mm	4.8 <i>d</i>	4.0 c	1.6 b	0.6 a	0.5 a	0.5 a	3.3 c	0.75
Lfw, mm	4.0 a 4.1 c	2.6 b	1.0 <i>a</i>	0.7 a	0.4 <i>a</i>	0.3 a	2.6 b	0.82
Lfw, mm	11.1 d	6.6 <i>abcd</i>	3.0 <i>a</i>	9.1 cd	4.7 abc	3.8 <i>ab</i>	6.9 <i>abcd</i>	4.7
Lig, mm	7.0 d	6.0 <i>cd</i>	2.6 a	4.1 <i>abc</i>	4.9 <i>bc</i>	3.8 <i>ab</i>	5.8 bcd	2.1
Ie (1-4)	3.5 a	3.0 a	2.9 a	3.2 a	3.3 a	3.6 a	3.5 a	1.1
1pd, cm	6.3 a	4.1 a	1.1 a	1.9 a	6.7 a	7.2 a	6.5 a	6.4
Ilb (no.)	4.8 <i>cd</i>	5.2 d	3.3 <i>abc</i>	4.5 bcd	3.0 <i>ab</i>	2.5 a	5.2 d	1.5
Ib (no.) Ih, cm	19 b	15 b	5.5 av	18 b	19 b	17 b	19 b	5.0
lw, cm	19 <i>b</i> 18 <i>b</i>	13 b	5 a	18 b	18 b	17 b	16 b	8.2
lh:Iw	1.11 a	1.13 a	1.73 a	1.30 a	1.72 a	1.36 a	1.36 a	1.9
III.Tw Ia (1-4)	1.11 a 1.2 ab	1.15 a	2.0 b	3.1 c	1.5 ab	1.50 ab	1.7 <i>ab</i>	0.88
· · ·	3.8 <i>ab</i>	3.0 <i>a</i>	4.4 <i>ab</i>	2.7 a	5.0 b	4.9 b	4.2 ab	1.8
Ipc $(1-5)$		1.6 ab	2.9 c	1.5 a	2.2 bc	-2.6 c	1.3 a	0.81
Sa (1-3)	1.6 ab	2.1 a	3.9 <i>ab</i>	2.4 a	4.9 b	4.1 <i>ab</i>	3.8 <i>ab</i>	2.0
Sc(1-5) = Sc(1-4)	2.7 a	1.6 a	3.9 av	3.0 <i>bc</i>	3.3 bc	3.1 bc	2.5 ab	0.97
Sg(1-4)	2.7 bc	5.2 bc	3.6 a	4.5 b	5.6 cd	6.0 d	7.1 e	0.75
Glt, mm	5.1 bc			4.3 <i>b</i> 4.2 <i>b</i>	5.5 cd	5.9 d	6.9 e	0.73
Glb, mm	5.1 c	5.2 <i>cd</i>	3.4 a	4.2 b 0.33 d		0.11 abc	0.9 e	0.18
Gls, mm	0.07 <i>ab</i>	0.00 a	0.20 b		0.11 abc	2 ab	0.28 cu 4 bc	3.3
Glsp, %	1 ab	0a	6 cd	7 d 4.3 b	2 ab 4.9 bc	5.2 c	6.1 d	0.66
Gut, mm	4.8 bc	4.8 bc	3.5 a					0.66
Gub, mm	4.7 b	4.8 <i>b</i>	3.4 a	4.0 a	4.8 b	5.1 b	5.9 c	
Gus, mm $V_{(0,2)}$	0.07 <i>ab</i>	0.04 a	0.16 ab	0.28 c	0.08 ab	0.09 <i>ab</i>	$0.21 \ b$	0.15
K (0-3)	1.9 b	2.2 b	2.8 a	1.9 <i>b</i>	1.7 <i>b</i>	1.9 <i>b</i>	1.9 b	0.69
M (0-2)	0.9 b	1.5 c	0.6 <i>ab</i>	1.6 c	0.1 a	0.3 ab	0.1 a	0.64
Glt:Gut	1.07 <i>ab</i>	1.08 abc	1.00 a	1.06 a	1.14 cd	1.15 cd	1.17 d	0.069
Lt, mm	3.2 <i>a</i>	3.2 a	2.8 a	3.5 <i>ab</i>	4.0 bc	4.4 c	3.9 bc	0.64
Lb, mm	2.7 a	3.1 <i>abc</i>	2.7 a	2.9 <i>ab</i>	3.2 bc	3.4 c	2.9 <i>ab</i>	0.45
Ls, mm	$0.50 \ bc$	0.08 a	0.32 <i>ab</i>	$0.59 \ bc$	0.76 cd	1.01 d	1.04 d	0.31
Lsp, %	15 bc	3 a	11 b	17 cd	19 cd	23 de	26 e	6.0
B (0-4)	0.0 a	0.0 a	0.0 a	0.0 a	0.0 <i>a</i>	3.8 <i>b</i>	4.0 c	0.22
Rc (0-3)	2.0 d	1.9 <i>d</i>	0.4 b	3.0 e	1.1 c	1.0 c	0.0 a	0.26
Rd (0-3)	1.4 b	1.1 b	0.3 a	2.7 c	3.0 c	$1.0 \ b$	0.0 a	0.49
Pt, mm	2.2 a	2.4 <i>ab</i>	2.5 ab	2.7 b	3.4 c	3.5 c	2.5 ab	0.43
Pb, mm	2.1 a	2.4 <i>ab</i>	2.4 <i>ab</i>	2.5 bc	2.8 cd	3.0 d	2.4 <i>ab</i>	0.39
Ps, mm	0.07 <i>ab</i>	0.02 a	0.02 a	0.19 b	0.57 c	0.57 c	0.08 ab	0.15
Psp, %	3 ab	1a	1 a	7 b	17 c	16 c	3 ab	4.3
Re, mm	2.3 ab	2.6 bc	2.1 a	2.3 <i>abc</i>	2.6 bc	2.8 c	2.6 bc	0.45
At, mm	7.0 c	0.7 a	2.3 b	5.8 c	8.9 <i>d</i>	$10.0 \ de$	10.7 e	1.3
Ac, mm	2.7 c	0.0 a	0.0 a	2.1 b	3.5 d	3.9 d	3.6 d	0.52
Ab, mm	4.3 c	0.7 <i>a</i>	2.3 b	3.8 c	5.4 d	6.0 d	7.1 e	1.0
Abp, %	62 ab	100 c	100 c	65 ab	60 a	60 a	66 <i>b</i>	4.7
Aa, mm	1.2 b	2.8 c	2.6 c	1.2 b	0.6 a	0.6 a	1.4 b	0.27
Aap, %	39 b	88 c	89 c	33 b	15 a	14 a	36 b	6.0
A, mm	0.74 <i>ab</i>	0.66 a	0.68 a	0.62 a	1.28 c	1.28 c	0.92 <i>b</i>	0.24

inflorescences shorter (many larger inflorescences had disarticulated at the time of collection). These differences are likely to be due to most of the examined specimens being mature to very mature (see discussion for Age Effects). The outer glumes had more eiliated margins than for var. *billardierei* and while lemma setae were shorter, lemma bodies were longer on average.

Agrostis billardierei var. collicola

Sixty eight percent of characters were significantly different between this taxon and var. *billardierei* (with fifty percent for LSD at 0.1%). Except for the culm height to total height percent (Chp), all the vegetative characters were significantly smaller; total plant, tussock and culm heights and leaf widths being diagnostically distinct. Inflorescences and spikelets were also significantly smaller than var. *billardierei*, although the largest examples of var. *collicola* did exceed the smallest examples of the type variety. Despite the smaller spikelets, the lemmas (and paleas) of var. *collicola* displayed a similar size range to var. *billardierei*; mean lower glume:lemma length (including setae) being 1,20 for the former and 1.62 for the latter.

Apart from the diagnostically distinct, short awns and near terminal awn attachment, var. *collicola* generally possessed glumes with dense, finely scabrid surfaces (extending from keels to near margins) and lemmas with almost completely smooth surfaces. The glumes of var. *billardierei* and var. *tenuiseta* (apart from the keels) were generally smooth or with occasional scattered scabrid projections and the lemmas normally had at least some microscopic scabrid projections near the central nerve.

The awns of var. *collicola* were significantly longer than for var. *tenuiseta* and tend to be decurrent from the lemma back, rather than having a column (even a minute one, as is often the case in var. *tenuiseta*).

Agrostis billardierei var. robusta

Fifty six percent of characters were significantly different between this taxa and var. *billardierei* (thirty four percent being for LSD at 0.1%). As well as the diagnostic characters of narrower and inrolled leaves and distally densely coarse scaberulous lemmas, var. *robusta* was significantly different from var. *billardierei* in its shorter ligules, less stiff inforescences, shorter glumes and awns, longer paleas, longer glume and palea setae and glumes with greater ciliation of margins. However, the currently used diagnostic character of more scabrous keels of the outer glumes was not distinct between the two taxa. Contrary to previous descriptions (Vickery 1941, Walsh & Entwisle 1994) there was little evidence of scabrid projections on the sides of the glumes, except very occasionally and then distally scattered. Examination of the holotype agreed with this finding. There were no obvious character differences between the coastal and inland specimens for either taxon.

Besides the generally distinct scabridity of the distal surfaces of the lemmas and the narrow leal width and inrolling of var. *robusta*, a few other characters could be useful in identifying this taxon. For example, ligule length could be a guide. Sixty nine percent of var. *billardierei* had ligules greater than 5 mm (with 53% greater than 6 mm) compared to only 13% of var. *robusta* (with none greater than 6 mm). Another useful character is the length of the outer glume setae expressed as a percent of the total glume length (Glsp). Seventy three percent of var. *robusta* had Glsp greater than 5% compared to none for var. *billardierei*.

Agrostis billardierei var. filifolia

This taxon was separated from var. *billardierei* in sixty four percent of measured characters (forty eight percent being for LSD at 0,1%). The main diagnostic character which separated var. *filifolia* from var. *billardierei* and var. *robusta* was its near-basal awn attachment (8 to 23% of lemma length with a mean of 15%) compared to mid-back attachment (29 to 47% with a mean of 39% for var. *billardierei* and 23 to 45% with a

mean of 33% for var. *robusta*). The taxon was also clearly separated from var. *billardierei* by its narrow leaves and longer palea setae (0.3 to 1.2 mm compared to 0.0 to 0.2 mm). Although the ranges in palea setae length overlapped between var. *filifolia* and var. *robusta*, only 4% of var. *robusta* specimens exceeded 0.3 mm compared to 88% of var. *filifolia* specimens. The lemma surface often served to distinguish these three taxa. While the lemma of var. *filifolia* was uniformly minutely granular-papillose to scaberulous, the lemma of var. *filifolia* was sparsely and minutely granular to scaberulous on the keel and distal part of the lemma, and var. *robusta* was generally strongly and densely scaberulous in the distal part of the lemma extending down the keel (although this character was occasionally found to be less obvious in very mature or stunted specimens). In both vars. *billardierei* and *robusta*, the lemma was almost completely devoid of scabrosities on the proximal lateral surfaces.

Other significantly different but non-diagnostic characters separating var. *filifolia* from var. *billardierei* were its shorter basal tussock, shorter flag leaves, shorter ligules, less branched inflorescence, more purple spikelets, larger lemmas, paleas, awns and anthers and less ciliated glume margins.

In addition to its diagnostically distinct characters, var. *filifolia* differed significantly from var. *robusta* in having shorter culms, shorter flag leaves, less branched, stiffer, less crowded and more purple inflorescences and larger glumes, lemmas, paleas, awns and anthers. Setae points on glumes, lemmas and paleas were longer but glume margins were less ciliated. Although both taxa had narrow leaves, var. *filifolia* leaves were either flat, conduplicate or pseudo-convolute, in contrast to the strongly involute to convolute leaves of var. *robusta*.

Agrostis aemula var. setifolia

This taxon was diagnostically separable from var. *aemula* in its longer palea setae (0.3 to 0.9 mm compared to 0.0 to 0.3 mm) and lower awn attachment (8 to 26% compared to 25 to 46%). It was also distinct, on the basis of leaf width (0.2 to 1.0 mm compared to 2.0 to 4.5 mm). The taxon also differed from *A. aemula* var. *aemula* in its significantly shorter ligules (Lig), lesser branched panicles, less clustered spikelets, shorter glumes², glume setae and awn bristles and longer lemmas, paleas and anthers. The lemmas were also slightly less hairy on average.

Apart from its hairy lemmas, A. aemula var. setifolia differed statistically from A. billardierei var. filifolia only in a few floret characters. including slightly longer lemma setae and awns.

AGE EFFECTS

Table 3 summarises the results of ANOVA analysis for each taxon according to age class (see Methods for descriptions). The effects of plant age (as defined by inflorescence age) was greatest for *A. billardierei* var. *filifolia*, *A. aemula* var. *setifolia* and *A. aemula* var. *aemula*. Little or no effect was seen for *A. billardierei* var. *billardierei* or *A. billardierei* var. *tenuiseta*. Obviously the uneven numbers of specimens in each age class for some taxa inhibits detailed assessment but some trends are evident.

Significant differences resulted from analysis of overall plant height, tussock height and culm height for a number of taxa. In general, the relative heights to overall height for tussocks and/or culms decreased with age. For *A. billardierei* var. *filifolia*, *A. aeuula* var. *setifolia* and *A. aeuula* var. *aeuula*, this was the result of increasing overall plant height with age, at least to the 'mature' age. At the 'ripe' age for these taxa and for both the 'mature' and 'ripe' ages of *A. billardierei* var. *robusta*, overall height was less on average than for

² It is recognised that smaller spikelet forms of *A. aemula* var. *aemula* (e.g. 3.6 to 5.5 mm, as reported by Walsh and Entwisle 1994) are likely to have glume lengths similar to or shorter than those of var. *setifolia*.

Taxon	bi	illardierei	tenuiseta	collicola	robusta	filifolia	setìfolìa	aemula
Age	I	1	0	2	4	9	4	5
	G	4	2	2	17	16	19	6
	М	12	3	4	28	17	5	5
	R	9	6	0	14	2	5	4
Vegetative	Hgt			*		**	*	**
Character	Llhp			*			*	*
	Chp				*	**		***
	Lr		**					
Inflorescence	Iw				**	***	***	**
Character	Ia				*	***		
	lpc			**			**	***
	Sa					**		
Spikelet	Sg				*		***	**
Character	Glt					**		
	Ls					**		
	Ps					**		*
	At					*	*	
	Aa							*

Table 3. Number of specimens assessed for each age class of the currently recognised taxa (represented by varietal epithet only) and measured plant characters showing significant differences (*** = $P \le 0.001$, ** = $P \ 0.001$ to $P \ 0.01$, * = $P \ 0.01$ to $P \ 0.05$) with age.

I = immature, G = maturing, M = mature, R = ripe

younger aged plants and either reflects an earlier maturing of smaller and less robust plants or the disarticulation of early and taller inflorescences than those still present and able to be assessed by the study. Although relative tussock height was also significantly different for *A. billardierei* var. *collicola* (between taller immature plants and smaller maturing plants), the results are based on too few specimens to have any validation.

Leaf roll increased with age for *A. billardierei* var. *tenuiseta* but only to a value of 2 (i.e. some leaves displayed slight inrolling). Other characters, thought to be associated with age, such as flag leaf length, inflorescence height and spikelet gape were not significantly different, but this result may just reflect the small numbers of specimens assessed by ANOVA and the lack of any immature specimens.

Panicles of *A. billardierei* var. *robusta* and *A. billardierei* var. *filifolia* showed significant stilfening with age and, along with the varieties of *A. aeuula*, broadened with age, as expected. Increasing age significantly increased the purpling of the panicles and/or spikelets of *A. billardierei* var. *collicola*, *A. aeuula* var. *setifolia* and *A. aeuula* var. *aeuula*.

The generally gaping glumes of 'immature' spikelets of *A. billardierei* var. *robusta* and the two *A. aeuula* varieties progressively closed with age. The same trend was noted for *A. billardierei* var. *filifolia* but was not significant.

The glumes, lemma setae, palea setae and awns of *A. billardierei* var. *filifolia* showed significantly decreased sizes as age progressed. The same trends were observed in *A. aeuuula* var. *setifolia* for glumes and awns but only awns were significantly different. Delicate structures such as awns and setae points are likely to show reduced length with age, due to broken or withered tips, but the reduced glume length cannot be explained by the same process (no changes to glume setae length were evident). Mean glume lengths for *A. billardierei* var. *filifolia* were 6.0, 5.7, 5.3 and 5.2 mm for 'immature', 'maturing', 'mature' and 'ripe' specimens respectively, representing a 13% reduction overall. Further

study would be required to ascertain whether this is a real reduction in size with age or an artefact of the collection process (i.e. the same plant populations were not represented in each age class).

Agrostis aemula var. aemula also shows significant differences in palea setae length, but these do not follow a trend in one direction. Awn attachment height significantly increased with age in this species, despite no change in lemma length. This again, may be an artefact of the collection process.

EXAMINATION OF HERBARIUM SPECIMENS

Fifty eight percent of the herbarium specimens examined had been determined as *A. billardierei* var. *billardierei*. Comparison with the type confirmed 135 of these determinations. This included six specimens from Kangaroo Is. (Cape de Couedic and Rocky River N.P.), despite their small stunted appearance (about 15 cm tall with flat leaves, 2-3.5 mm wide), very short, often enclosed panicles and generally smaller than average spikelets. Vickery, on her determination label, regarded one of these specimens as 'a form' of var. *billardierei* (Rocky River, *J B Cleland*, 24 Nov. 1945, AD *96243134*).

Three specimens determined as *A. billardierei* var. *billardierei* were found to be *A. aemula* var. *aemula* while the reverse was true for a further six specimens. Superficially, these 2 taxa are similar in habit and leaf character. Even the type sheet has both taxa mounted on it (*R Br. 6218*, 1802-05, BM), a mistake referred to in the earlier revision (Vickery 1941).

An additional 25 specimens were found to be incorrectly determined as *A. billardierei* var. *billardierei*. These included five specimens of *A. avenacea* with glabrous lemma backs (but hairy sides), three of *A. venusta* Trin., one each of *A. capillaris* L. var. *arista-ta* (Parnell) Druce (syn. *A. castellana* Boiss. & Reut.; Batson 1998) and *A. billardierei* var. *filifolia*, three of *A. billardierei* var. *tenuiseta* and 12 of *A. billardierei* var. *robusta*. All of these taxa have lemmas with hairless backs like *A. billardierei* var. *billardierei*, and because of their comparative rarity, are likely to have been overlooked or not considered during determination. Some confusion between var. *billardierei* and var. *robusta* was evident for a number of South Australian and Tasmanian specimens. Some specimens of var. *billardierei* (often inland collections) had distally finely scaberulous lemmas, not unlike some lesser scabrid forms of var. *robusta* (e.g. specimens from the Boomer Marsh/Marion Bay/Maria Is. region of Tasmania). In these cases, other characters (e.g. leaf width) were used for diagnosis.

Most of the specimens determined as *A. billardierei* var. *robusta* (15 of 17) and *A. aemula* var. *setifolia* (18 of 19) were confirmed. Although the types for these taxa have contracted, just-emerging inflorescences and the basal leaves are partially senescent and therefore rather stiff, spikelet features serve as good diagnostic characters. Nevertheless, for each of these taxa, three specimens had been incorrectly determined as *A. aemula* var. *aemula*.

Only 12 of 23 specimens determined as *A. billardierei* var. *filifolia* conformed to the type. The remaining specimens were referable to *A. billardierei* var. *robusta* (5), *A.* aff. *avenacea* (2), *A. venusta* (2) or *A. aemula* var. *setifolia* (2). A number of stunted specimens from near-coastal south-east South Australia were difficult to place. They had low awn insertion points like *A. billardierei* var. *filifolia* but rather small and crowded spikelets, scabrid lemmas and inrolled leaves like var. *robusta*. Vickery regarded one of these as 'a peculiar form' of var. *filifolia* (Cape Banks, *J B Cleland*, 27 Nov. 1945, AD 97222340).

CONCLUSION

The results of the statistical analyses of the survey specimens and examination of herbarium specimens are evidence of a taxonomic position supporting all the currently recognised taxa, but at levels and in combinations different from those currently accepted. An arrangement that is concordant with the analyses has:

(1) A. aenula var. setifolia specifically distinct from A. aenula var. aenula

(2) A. billardierei var. filifolia and A. aenula var. setifolia as varieties of the same species (3) A. billardierei var. billardierei, A. billardierei var. robusta, A. billardierei var. collicola and a taxon including A. billardierei var. filifolia and A. aenula var. setifolia recognised as separate species.

Agrostis billardierei var. tenuiseta has a number of distinct characters that separate it from A. billardierei var. billardierei, but PCO and cluster analysis suggest a varietal relationship rather than a specific one.

Although A. *aenula* var. *aenula* is superficially similar to A. *billardierei* var. *billardierei* in vegetative form, there appears to be sufficient spikelet differences (apart from hairy lemmas) to maintain their separate specific status.

The appropriate combinations and new species descriptions are made in the following section.

Taxonomy

KEY TO TAXA TREATED IN PRESENT STUDY

- 1. Leaves greater than 2 mm wide and flat......2
- Awn greater than 3.5 mm long, inserted just below lemma mid-back, exceeding the glumes......la. A. billardierei var. billardierei

- 4. Awn inserted within lower 1/4 of lemma, palea setae mainly 0.4 mm long or more,

TAXON DESCRIPTIONS

The following descriptions are an expansion of those provided by Walsh and Entwisle (1994) and Morris (1990). A selected list of examined specimens accompany each taxon description while a full list of examined specimens is available from the senior author for interested readers.

1. *Agrostis billardierei* R. Br., *Prodr.* 171 (1810). *Type:* New South Wales, Port Jackson, 1802-05, *R Brown* (holotype BM).

Mid to dark green (sometimes bluish-green), tufted, glabrous, *pereuuial* (may be annual under unfavourable conditions), 25–75 cm tall (including inflorescences but these sometimes overtopped by leaves); culms ascending or crect, 15-40(-50) cm long. *Leaf* blades rather stiff, scabrous, flat (sometimes folded or loosely inrolled on drying); basal leaves (often forming a flattened tussock) 15–40 cm long, (2-)3-7 mm wide: ligules obtuse, 3-12 mm long. *Inflorescence* generally a rather stiff, open paniele with erect to spread-

ing branches, 10–30 cm long, 5–30 cm wide, its base enclosed by the upper leaf sheath or its lower branches becoming free with maturity; peduncle 2–15 cm long if visible; 2–7 branches in the lowest whorl; spikelets generally partly overlapping. *Spikelets* (3.0–)4.0–6.5(–7.0) mm long overall (excluding awn); glumes acuminate, subequal, keeled; lemma 2.5–4.5 mm long overall, hairless except for callus tuft and more or less shining (often with scattered, very fine to microscopic scabrid projections in the upper half and near the central nerve in the lower half but sometimes distally finely scaberulous), with 2–4 setae at apex; palea 1.5–3.0 mm long overall, narrowly and very shortly bifid at the apex (points to 0.2 mm long); rachilla extension forming a plumose bristle (1.5)–2.0–3.0 mm long (including hairs); anthers 0.5–1.0 mm long. **Coast Blown-grass**.

1a. Agrostis billardierei var. billardierei

Sometimes shortly rhizomatous. Flag *leaves* to 20(-30) cm long, 2-5(-8) mm wide. *Panicle* branches and pedicels and spikelets usually purple to dark or reddish-purple (even at inflorescence emergence) but fading to dull brown with age. Mature *spikelets* more or less gaping. Glume apex occasionally with a fine seta to 0.3 mm long, moderately scabrous along the keel and often lightly scaberulous on the sides, margins entire or with a few scattered cilia; lemma setae 0.2-1.0 mm long; awn fine, bent, (3.5-)5.0-9.0 mm long, well exceeding the glumes, attached 30-45% from the lemma base.

Distribution: Widely distributed along the coast in south-eastern Australia from the vicinity of Grafton in New South Wales, to at least as far west as Port Lincoln, South Australia with a few scattered inland occurences (e.g. Little Desert in Victoria), and in Tasmania occurring virtually all around the coast (including Bass Strait islands) (Fig. 6). Also occurring through coastal areas of New Zealand except the far north (Kermadec Is) and, apparently, the south-western part of the South Island. (Fig. 6)

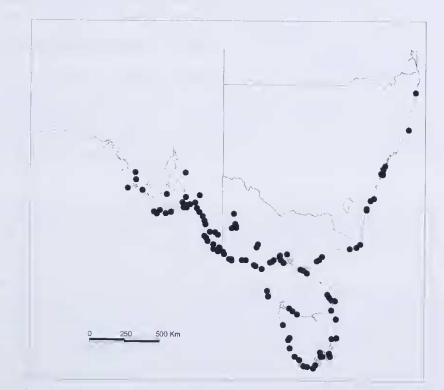


Figure 6. Distribution map of known collections of *Agrostis billardierei* var. *billardierei* in SE Australia.

Ecology: See general notes on habitat and phenology following taxonomic section.

Selected specimens examined: SOUTH AUSTRALIA: Port Elliot, 15 Jan. 1913 (AD); Harriet River, Kangaroo Is., 7 Oct. 1922, Oshorn (AD); Port Lincoln, 17 Dec. 1941, Cleland (AD); 10 km west of Naracoorte, 18 Nov. 1961, Hunt (AD); Bankers Knoll, Younghusband Penin., 15 Dec. 1981, Williams 12180 (AD, MEL); Warooka, 16 Nov. 1989, Brown 455 (MEL, HO); near mouth of Marne River, 19 Dec. 1995, Spooner (AD). NEW SOUTH WALES: Port Macquarie, Nov. 1915, Boorman (NSW); Cave Beach, 4.8 km SW Jervis Bay, 12 Oct. 1971, Coveny 3683 (NSW); North Headland, Wamberal, 10 Nov. 1973, Jacobs 638 (NSW); Long Beach, Batcmans Bay, 18 Nov. 1991, Crawford 1413 (NSW, MEL). VICTORIA: Wingan Inlet N.P. west of mouth, 23 Nov. 1969, Beauglehole and Finck 32002 (MEL, NSW); Cape Shanck, 3 Dec. 1970, Todd 27 (MEL); Point Lonsdale, 10 Dec. 1983, Albrecht 694 (MEL); Little Desert N.P., 18 Dec. 1983, Carr 7704 (MEL); Walkerville North, 5 Dec. 1994, Paget 1146 (MEL); St. Marnock's Swamp, Crossroads, south of Eurambeen, 4 Jan. 1996, Brown 1117 (MEL). TASMANIA: South Port, Jan. 1850, Stuart (MEL); Eaglehawk Neck, 15 Jan. 1949, Blake 18281 (HO); Wybalenna Is., off Flinders Is., 12 Dec. 1968, Harris (HO); Rocky Cape, 7 Jan. 1977, Mason 13249 (HO); Peron Dunes, St. Helens Point, 7 Jun. 1983, Buchanan 1196 (HO); Turua Beach, Deadmans Bay, 21 Jan. 1987, Moscal 14225 (HO, MEL); Planters Beach, Cockle Creek, 2 Feb. 1998, Buchanan 15056 (HO).

1b. *Agrostis billardierei* var. *tenuiseta* D. Morris, *Muelleria* 7: 147 (1990). *Type*: Tasmania, Dolphin Sands, Nine Mile Beach, 10 Dec. 1984, *Buchanan* 4763 (holotype HO; isotype NSW).

Often rhizomatous. Flag *leaves* to12 cm long, (1.5–)3–4 mm wide. *Panicle* branches, pedicles and spikelets mainly green tinged with purple but fading to straw with age. Mature *spikelets* hardly gaping. Glume apex without a fine seta or to 0.1 mm long, moderately to strongly scabrous along the keel and often lightly scaberulous on the sides, margins ciliated; lemma setae to 0.2 mm long or absent; awn very fine, straight or slightly curved, 0.5–2.5 mm long (sometimes absent), not or hardly exceeding the glumes, attached 70–95 % from the lemma base.

Distribution: Apparently confined to coastal areas in north-eastern Tasmania (including castern Bass Strait islands). (Fig. 7)

Ecology: See general notes on habitat and phenology following taxonomic section.

Selected specimens examined: TASMANIA: Clarkes Is., Furneaux Group, 26 Jan. 1966, Whinray 1572 (CANB), Babel Is., Furneaux Group, 22 Jan. 1967, Whinray 1764 (MEL); Whitemark, Flinders Is., Dec. 1975, Morris (HO); Passage Is., Furneaux Group, 6 Jan. 1979, Whinray (MEL); Kelvedon Beach, Great Oyster Bay, 28 Jan. 1999, Brown 1579 (MEL): Mayfield Beach, Great Oyster Bay, 28 Jan. 1999, Brown 1585 (MEL); Scamander Beach, Beaumaris, 15 Jan 2000, Brown 1595 (HO).

2. Agrostis collicola (D. Morris) A.J. Brown & N.G. Walsh, *stat. nov. Agrostis billardierei* R. Br. var. *collicola* D. Morris, *Muelleria* 7: 147 (1990). *Type:* Tasmania, Saddle between The Hippo and Moonlight Ridge Hill 3, 10 Feb. 1985, *Collier 309* (holotype HO).

Mid to dark-green, tufted, glabrous, weak *perenuial*, 10–20 cm tall (including inflorescences); culms erect, 5–10 cm long. *Leaf* blades flat to conduplicate (sometimes pseudoconvolute on drying); basal leaves (generally forming a small erect tussock or tuft) 5–15 cm long, 1–2 mm wide; flag leaves 1.5–7.5 cm long, 0.2–2.0 mm wide; ligules obtuse, 1.5–4.0 mm long. *Inflorescence* an open panicle with spreading branches, 2–9 cm long, 4–9 cm wide, its base enclosed by the upper leaf sheath or its lower branches becoming free with maturity; peduncle 1-3 cm long if visible; 2–4 branches in the lowest whorl; branches and pedicels green, becoming purple with maturity; spikelets partly overlapping to not overlapping, generally gaping. *Spikelets* 2.5–4.0 mm long overall (excluding awn);

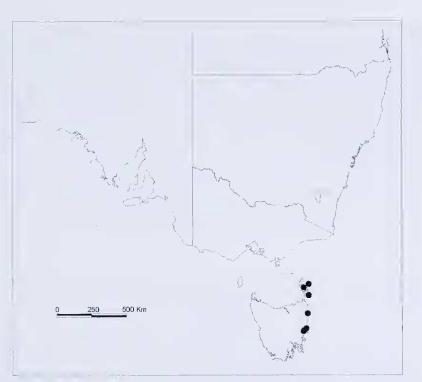


Figure 7. Distribution map of known collections of *Agrostis billardierei* var. *tenuiseta* in SE Australia.

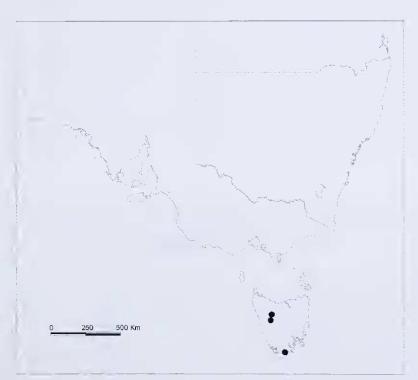


Figure 8. Distribution map of known collections of *Agrostis collicola* (syn. *Agrostis billardierei* var. *collicola*) in SE Australia.

usually purple (green when immature); glumes acuminate and keeled (generally the kcel extending to a fine seta up to 0.5 mm long), subcqual, moderately to coarsely scabrous along the keel and densely and finely scaberulous on sides, margins smooth or with a few scattered cilia; lemmas 2.5–3.5 mm long overall, hairless except for callus tuft, smooth, sometimes purple streaked, with 2–4 setae at apex 0.2–0.5 mm long; awn very fine, straight, dccurrent from central nerve of lemma, 1.0–3.5 mm long, attached 80–95% from the lemma base; palea 2.0–3.0 mm long (minutely bifid at the apex if at all); rachilla extension forming a plumose bristle 1.5–2.5 mm long (including hairs); anthers 0.4–0.8 mm long. Hill Blown-grass.

Distribution: Apparently confined to mountainous areas of Tasmania, from 800–850 m altitude (Fig. 8).

Ecology: See general notes on habitat and phenology following taxonomic section.

Selected specimens examined: TASMANIA: Lake Ewart, 7 Feb. 1987, Buchanau 10071, (HO); Lake Will south of Barn Bluff, 15 Jan. 1989, Collier 3941, (HO).

3. *Agrostis robusta* (Vickery) A.J. Brown & N.G. Walsh *stat. nov. Agrostis billardierei* R. Br. var. *robusta* Vickery, *Contr. New South Wales Natl Herb.* 1: 110 (1941). *Type:* Victoria, Melbourne, 17 Nov. 1853, *Adamson 224* (holotype K).

Mid to light-green (new shoots can be bluish-green), tufted, glabrous, *annual* or *peremi-al*, 25-75 cm tall (including inflorescences); culms ascending or ercct, 10–55 cm long. *Leaf* blades rather stiff to lax, scabrous, convolute to strongly involute (sometimes flattening with age); basal leaves (sometimes forming an ercct tussock) 10–50 cm long, 0.2-1.0(-1.5) mm wide; flag leaves 2.5-15(-35) cm long, 0.2-1.0(-1.5) mm wide; ligules obtuse, 2-7 mm long. *Inflorescence* an open panicle with spreading to lax branch-

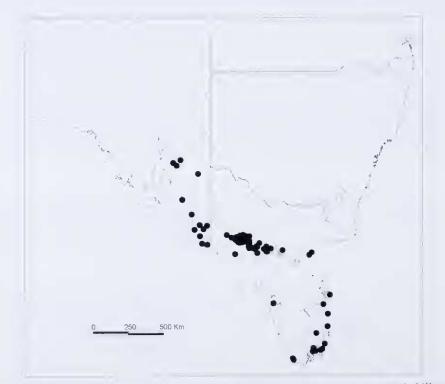


Figure 9. Distribution map of known collections of Agrostis robusta (syn. Agrostis billardierei var. robusta) in SE Australia

es (except at maturity), 10–25 cm long, 10–30 cm wide, its base enclosed by the upper leaf sheath or its lower branches becoming free in late maturity; peduncle 2-9 cm long if visible; 1-8 branches in the lowest whorl; branches and pedicels generally green to greyish-green or occasionally purplish-green; spikelets generally partly overlapping and more or less gaping. Spikelets 3.5–5.5 mm long overall (excluding awn), usually green to greyish-green; glumes acuminate and keeled (generally the keel extending to a fine seta 0.6(-0.8) mm long), subequal or the lower slightly longer, moderately scabrous along the keel but smooth on sides (very occasionally lightly and distally scaberulous), margins with a few scattered cilia to fully ciliated; lemma 2.5-4.5(-5.5) mm long overall, hairless except for callus tuft, rather firm, strongly scaberulous in the upper half or at least on and near the setae and nerves towards the more or less fluted apex, more or less shining in the lower half and devoid of scabrid projections except for near the central nerve, with 2-4 setae at apex 0.3–1.0 mm long; awn bent, (3.5–)4.5–7.0(–8.0) mm long, attached 25–45 % from the lemma base; palea 2.0-3.5(-4.0) mm long overall, narrowly and shortly bifid at the apex (points to 0.3(-0.5) long); rachilla extension forming a plumose bristle 1.5-3.0(-3.5) mm long (including hairs); anthers 0.4-1.0(-1.2) mm long. Salt Blowngrass.

Distribution: Scattered in coastal areas from near Seaspray (south-eastern Victoria) westward to the Goolwa Barrage in South Australia, extending to c. 100 km inland on saline soils. Also scattered along the Tasmanian coastline, particularly on the east coast. (Fig. 9)

Ecology: See general notes on habitat and phenology following taxonomic section.

Selected specimens examined: SOUTH AUSTRALIA: Eight Mile Creek, 3 Feb. 1942, Eardley (AD); Lake Bonney, Barmera, 17 Feb. 1947, Cleland (AD); Goolwa Barrage, 6 Jan. 1950, Cleland (AD); Lake Eliza, Little Dip N.P., 9 Dec. 1975, Brock 239 (AD); Alcock 33 (AD); Mongolata Hills, 27 May 1989, Bates 18551 (AD); between Gulnare and Spalding, 16 Nov. 1989, Bates (AD); Avenue, 25 Jan. 1999, Brown 1570 (MEL, AD); Naracoorte, 25 Jan. 1999, Brown 1572 (MEL, AD). VICTORIA: Glenthompson, 27 Jan. 1993, Heard (MEL); Skipton, 11 Jan. 1994, Brown 870 (MEL); Lake Corangamite, North Cundare, 16 Dec. 1994, Brown 973 (MEL); Woodbourne, 4 Jan. 1996, Brown 1130 (MEL); Ross Bridge, 8 Jan. 1996, Brown 1149 (MEL); Murtagurt Swamp, Barwon Heads, 24 Dec. 1996, Brown 1223 (MEL); Honeysuckle Estate, Seaspray, 17 Dec. 1998, Brown 1527 (MEL). TASMANIA: mouth of Boomer Creek, 12 Jan. 1941, Curtis (HO, MEL); St. Helens, 24 Dec. 1959, Burns 213 (HO); Point Lesueur, Maria 1s., 12 Dec. 1977, Brown 334 & 449 (HO); Bathurst Harbour, Celery Top Islands, 12 Apr. 1978, Kirkpatrick (HO); Calverts Lagoon, South Arm, 4 Feb. 1979, Morris 79104 (HO, MEL); Gull Reef, Port Davey, 10 Feb. 1980, McKendrick (HO); mouth of Harcus River, 27 Dec. 1986, Buchanan 8973 (HO); 4 km west of Harley's Point, Cape Barren Is., 12 Dec. 1988, Buchanan 11142 (HO); Cape Portland near Cape Lagoon, 7 Jan. 1993, Steane (HO).

4. *Agrostis punicea* A.J. Brown & N.G. Walsh *Nom. et stat. nov. Type:* Tasmania, New Norfolk, 15 Nov. 1840, *Ballantine 1446* (holotype K; isotype HO). *Agrostis billardierei* R. Br. var. *setifolia* Hook. f., *Fl. Tas.*, 2: 115 (1860). *Agrostis aemula* R. Br. var. *setifolia* (Hook.f.) Vickery *Contr. New South Wales Natl Herb.* 1: 116 (1941).

Bluish-green, tufted, glabrous, short-lived *perennial*, 20–65 cm tall (including inflorescences); culms erect, 10-30(-45) cm tall. *Leaf* blades rather stiff, scabrous, conduplicate to pseudo-convolute (sometimes becoming involute on drying); basal leaves (generally forming an erect to spreading tussock) 5-25(-35) cm long, 0.2-1.0 mm wide; flag leaves 1.5-10 cm long, 0.2-0.5(-1.0) mm wide; ligules obtuse, 2-8 mm long. *Inflorescence* a fine, open panicle with erect to spreading branches, 10-25(-30) cm long, 5-30 cm wide, generally well exserted from the upper leaf sheath; peduncle 2-20 (-25) cm long; 2-5branches in the lowest whorl; branches and pedicels very fine, often pinkish-purple to reddish-purple; spikelets rather few, generally not overlapping, widely gaping. *Spikelets* 4.5–7.0 mm long overall (excluding awn); usually purple to dark purple; glumes acuminate and keeled (occasionally the keel extending to a fine seta 0.4 mm long), subequal, moderately scabrous along the keel but smooth on sides (occasionally lightly and distally scaberulous), margins entire or occasionally with a few scattered cilia; lemma 3.0-5.0(-5.5) mm long overall, with 2–4 setae at apex 0.5–1.5 mm long; awn bent, attached 10–20(–25) % from the lemma base and often (particularly when immature) lying in a groove of the lemma along the central nerve; palea 2.5–4.5 mm long overall, narrowly bifid at the apex (points (0.3–)0.4–1.2 mm long); rachilla extension forming a plumose bristle (1.5–)2.0–3.5 mm long (including hairs); anthers 0.8–1.7(–2.1) mm long. **Purple Blown-grass.**

Etymology: The epithet, meaning reddish-purple in Latin, refers to the colour of the panicle branches which is conspicuous on flowering plants. The epithets *filifolia* and *setifolia* which might otherwise have been chosen are preoccupied at species level within *Agrostis*.

4a. Agrostis punicea var. punicea

Lemma covered in lower three-quarters with hairs, upper nerves and setae finely scabcrulous. Awns 7.5–12.5 mm long. The sizes of glumes, lemmas, paleas and rachilla extensions (including hairs) do not occur in the bottom 20 % of each range for the species.

Distribution: Scattered across the volcanic plain and Dundas Tableland of south-west Victoria, extending into south-east South Australia with isolated occurrences in near-coastal south Gippsland. Also scattered in the Tasmanian midlands. (Fig. 10)

Ecology: See general notes on habitat and phenology following taxonomic section.

Selected specimens examined: SOUTH AUSTRALIA: Cooloolie, 11 Nov. 1945. Crocker (AD);



Figure 10. Distribution map of known collections of Agrostis punicea var. punicea (syn. Agrostis aemula var. setifolia) in SE Australia.

Marshes Swamp, between Glencoe and Mt. Burr, 19 Jan. 1969, *Wilson 970* (AD); Tantanoola Forest, 23 Nov. 1991, *Bates 26388* (AD). VICTORIA: Steep Bank Creek, 1 Nov. 1982, *Corrick 8473* (HO, MEL); Hamilton, 3 Nov. 1982, *Corrick 8544* (HO, AD); Buckleys Swamp, 22 Dec. 1986, *Brown 72B* (MEL); Craigieburn, 10 Nov. 1989, *Frood* (MEL); Mullungdung State Forest, 2 Nov. 1995, *Paget 1609* (MEL); 12 km north of Sale, 27 Oct. 1997, *Paget 2941* (MEL); Beeac, 7 Dec, 1995, *Brown 1014* (MEL); Hexham, 15 Dec. 1995, *Brown 1047* (MEL); Mt. Pollock, 3 Dec. 1997, *Brown 1384* (MEL); Byaduk, 5 Dec. 1997, *Brown 1438* (MEL); Ripponhurst, 5 Dec. 1997, *Brown 1543* (MEL); Coojar, 25 Jan. 1999, *Brown 1575* (MEL). TASMANIA: Penquite, 9 Dec. 1844, *Gunn 592* (K); Ulverstone, 1912, *Burbury* (HO); 7 km west of Ross, 10 Dec. 1984, *Fensham* (HO); 1.5 km north-west of Pringle Hills, 24 Dec. 1984, *Fensham* (HO).

4b. Agrostis punicea var. filifolia A.J. Brown & N.G. Walsh comb. nov. Agrostis billardierei R.Br.var. filifolia Vickery, Contr. New South Wales Natl Herb. 1: 110 (1941). Type: Victoria, Hawkesdale, Dec. 1901, Williamson (holotype K).

Lemma hairless except for callus tuft, covered with very fine to microscopic papillosescabrid projections, upper nerves and setae finely scaberulous. Awns 6.0–10.0 mm long. The sizes of glumes, lemmas, paleas and rachilla extensions (including hairs) cover the full range for the species.

Distribution: Scattered in the western half of south-west Victoria and extending into south-east South Australia with isolated occurrences at Lyndhurst and Meerlieu in Gippsland. Also two old records from near Hobart in Tasmania. (Fig. 11)

Ecology: See general notes on habitat and phenology following taxonomic section.

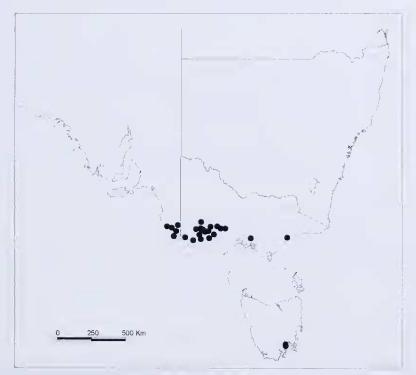


Figure 11. Distribution map of known collections of Agrostis punicea var. filifolia (syn. Agrostis billardierei var. filifolia) in SE Australia.

Selected specimens examined: SOUTH AUSTRALIA: near Mt. Gambier, 1880, von Mueller (MEL); Yallum and Beachport, Oct. 1883 (AD); Wooleys Lake, Beachport (?), Oct 1883 (AD); Penola, 27 Oct. 1945, Survey team (AD). VICTORIA: Buckleys Swamp, 22 Dec. 1986, Brown 72A (MEL); Connover Swamp, Drik Drik, 3 Dec. 1992, Albrecht 5159 (MEL, AD, HO); 12 km east of Woorndoo, 3 Dec. 1992, Albrecht 5189 (MEL); Lyndhurst, 19 Nov. 1993, Costello s.n. (MEL); Glenthompson, 10 Jan. 1994, Brown 827 (MEL); Hexham, 15 Dec. 1995, Brown 1046 (MEL); Hadden, 4 Jan. 1996, Brown 1123 (MEL); Lake Goldsmith, Stockyard Hill, 6 Dec. 1996, Brown 1189 (MEL); north of Karabeal, 13 Dec. 1996, Brown 1204 (MEL); Lake Repose, Glenthompson, 30 Dec. 1996, Brown 1246 (MEL); Dunkeld, 30 Dec. 1996, Brown 1241 (MEL); south of Bulart, 31 Dec. 1996, Brown 1270 (MEL); Moutjup, 14 Nov. 1997, Brown 1341 (MEL); Ballyrogan, 23 Dec. 1997, Brown 1473 (MEL); Homerton, 3 Dec. 1998, Brown 1517 (MEL); Meerlieu, 31 Dec. 1998, Brown 1539 (MEL). TASMANIA: Blackman's Bay, Feb. 1929, Rodway (HO); Hobart, 1929, Rodway (HO).

NOTES ON RELATED TAXA

Lachnagrostis tenuis (Cheeseman) Edgar, New Zealand J. Bot. 33: 30 (1995). Deyeuxia billardierei (R. Br.) Kunth. var. tenuis Petrie ex Cheeseman, Man. N.Z. Fl. 870 (1906). Type: New Zealand, Catlins River, Clutha Co., Otago, March 1896, H.J. Matthews (holo-type WELT; isotypes AK, WELT, CHR).

The 'Blown-grasses' of New Zealand have been separated from Agrostis L. into Lachnagrostis Trin. (Edgar 1995). This genus has 12 New Zealand species, with 2 of these (Lachnagrostis billardierei (R. Br.) Trin. syn. Agrostis billardierei R. Br., and L. filiformis (G. Forst) Trin. syn. Agrostis avenacea J.F. Gmel.) also found in Australia. Another species, Lachnagrostis tenuis (Cheeseman) Edgar which is not known from Australia, has many morphological characters in common with Agrostis robusta. In particular, it has narrow, strongly involute leaves and seaberulous lemmas. In general appearance, L. tenuis resembles smaller and less mature forms of A. robusta with its relatively small stature (20-30 em tall) and short leaves (5-15 em). It differs principally in its smaller and only partly spreading inflorescences (5-10 em long, 5-10 em wide) that are almost always enclosed at the base by the leaf sheath, and its shorter (1-2 mm long) ligules. Further, the lemma surface of L. tenuis is almost completely eovered with strongly scaberulous projections, whereas A. robusta is mainly scaberulous in the distal half only. Lachnagrostis tenuis has only been recorded from near-coastal latitudes south of 43° (Canterbury on South Island) whereas Agrostis robusta extends from 43° (southern Tasmania) to 33° (North Lofty Region of South Australia). However, like A. robusta, it is recorded as growing in salt marshes and tidal ground. Further study is needed before a definite conclusion can be reached on the correct placement of these taxa. Research on the generic limits of Agrostis and related genera (in particular, Deyeuxia) are in progress (S.L.W. Jacobs, New South Wales Herbarium, pers. comm.) and the results of this study may recommend the transferral of several native taxa into other genera. This work should include a reassessment of A. robusta and L. tenuis. Current knowledge suggests that these two entities could be recognised at infraspecific rank only.

Specimens examined: NEW ZEALAND, SOUTH Is.: Catlins River, Otago, D. Petrie, Mar. 1896 (WELT): Fortrose, Southland. D. Petrie, 4 Jan. 1913 (WELT); Lyttleton Harbour near Teddington., 2 Jan. 1966 (CHR); STEWART IS. Near head of South-west Arm, H.D.Wilson and C.D. Meurk, 18 Feb. 1980 (CHR).

Growth Habit and Habitat

GENERAL OBSERVATIONS

Agrostis billardierei var, tenuiseta has a very similar growth appearance to var. billardierei except that it appears to have a greater tendency to produce rhizomes. This habit is particularly noticeable where the taxon is growing on deep wind-blown sand, such as on the edge

of the seaward side of a sand dune. In Tasmania, var. *tenuiseta* has only been found, thus far, growing in stands of the introduced *Ammophila arenaria*, close to the beach, either on or between the first two or three sand dunes. In contrast, var. *billardierei* tends to grow in more sheltered positions, such as in tall grass or shrub communities in the depressions between sand dunes, on grassy (*Poa, Austrostipa* spp.) flats behind the sand dune complex or in cliff-top coastal scrub. Where it occasionally grows in more exposed positions, it is generally stunted and inflorescences ripen before exsertion from the leaf sheaths.

Observations of growth habit for *A. billardierei* var. *billardierei* and *A. robusta* have found that contrary to published descriptions (as *A. billardierei* var. *robusta*), *A. robusta* is more likely to have a less rigid habit than *A. billardierei*. However, habit is variable, depending on habitat. Where *A. billardierei* is found growing in more exposed situations or on saline flats, leaves, culms and mature panicles tend to be erect and rather stiff, compared to the more lax leaves and ascending culms of the smaller plants growing in the shelter of *Leptospermum/Acacia* thickets. *Agrostis robusta* can form erect and dense tussocks where soil moisture levels are more or less permanent, but generally it occurs as a weeping tussock with few culms. In both habitats, the leaves and panicles are more or less lax until the onset of senescence. *Agrostis robusta* is always found on saline flats or marshes and often in association with other salt-tolerant species such as *Puccinellia* spp., *Juncus kraussi, Plantago coronopus, Triglochin striata* and *Sarcocornia quinqueflora*.

Agrostis punicea var. punicea and var. filifolia have a similar range of habitats and are sometimes found mixed together in the same population. Their appearance in the field is identical and only examination of the lemma can discern the difference. Their fine, waving panicles can often be overlooked in a field of other grasses and herbs, unless they are a dominant species in the community. These taxa have been found growing in moist depressions in grasslands of *Themeda*, *Austrostipa* and *Austrodanthonia* spp., on the edges of non-saline swamps and on saline flats.

Agrostis collicola has been collected from exposed situations with little vegetation or from herb lawns on stream banks (Morris 1990).

SOIL CHARACTERISTICS

Table 4 shows soil analysis data for a range of *A. billardierei* var. *billardierei*, *A. robusta* and *A. punicea* sites sampled during January 1998 or 1999. Surface soil textures vary widely for each taxon. Means of electrical conductivity (and calculated total soluble salts) and soil moisture contents are similar for *A. billardierei* var. *billardierei* and *A. punicea* with data for both taxa ranging from low to moderate levels. Soil salts and moisture means and ranges for *A. robusta* are considerably higher than for the other two taxa. However, soil pH means (moderately alkaline) and ranges for *A. robusta* are similar to *A. billardierei*, while *A. punicea* has a lower mean value (slightly acid).

Taxa	No. sites	Soil texture range	pH _w	EC	TSS	M _d
A. billardierei var. billardierei	6	sandy loam to light clay	8.3 (6.8–9.6)	0.73 (0.15–1.7)	0.22 (0.04–0.50)	30 (11–48)
A. robusta	7	fine sandy clay loam to light clay	8.0 (7.7–8.7)	2.9 (1.5–5.7)	0.85 (0.45–1.7)	89 (46–269)
A. punicea var. filifolia	5	organic loam to light medium clay	6.5 (5.7–8.7)	0.74 (0.11–2.0)	0.22 (0.03–0.60)	38 (15–52)

Table 4: Range in soil texture, mean and range in soil pH in water (pH_w) , electrical conductivity
(EC) dS/m, total soluble salts (TSS) % and moisture content on dry soil basis (M_d) %
for various Agrostis spp. sites, sampled in January 1998 and 1999.

PHENOLOGY

Inflorescence emergence and maturing for all taxa varies according to environmental conditions but some general observations can be made. *Agrostis punicea* plants tend to mature earlier than those of *A. billardierei* var. *billardierei* or *A. robusta* but similar to *A. aemula*. In general, inflorescences of these taxa can start to appear during late October, are fully expanded by mid November and have mostly disarticulated by the end of December. Inflorescences of *A. billardierei* var. *billardierei* become noticeable during mid to late November and are mature by the end of December, although some younger panicles may also emerge at this time if conditions are favourable. *Agrostis robusta* generally does not show any inflorescences until mid December with new inflorescences emerging right up to the end of March if soil moisture is adequate. Maturity generally peaks around mid February.

LONGEVITY

The percentage of tussocks tagged in January 1998 that survived (i.e. grew new shoots and developed new inflorescences) through to January 1999 varied from site to site. For the two sites of *Agrostis robusta*, results were 44% and 100% survival. Survival rates dropped to 13% and 50% respectively over the following season. The latter site borders an area inundated with water all year except for mid summer, although even at that time, the soil remains wet. The former site, while remaining moist, is drier over the summer. Results of tussock survival for *A. puticea* were 80% and 100% after the first season but only 47% and 15% respectively after the second season. Both these taxa appear to be short-lived perennials, given favourable conditions. A few tussocks marked at two sites of *A. billardierei* var. *billardierei* were still growing vigorously when observed two years later and attest to the perennial nature of this taxon.

Acknowledgments

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Plant part	Measured and derived characters	Multivariate analysis	Variable type
Total	Total height (Hgt)	Yes	*C
	Basal tussock height (Llh)	Yes	C
	% basal to total height (Llhp)	No	Č
	Culm height (Ch)	Yes	C
	% culm to total height (Chp)	No	C
Leaves	Inrolling or folding (Lr)	Yes	**D (1-5)
	Basal width (Llw)	Yes	C
	Flag width (Lfw)	Yes	С
	Flag length (Lfh)	Yes	C
	Ligule length (Lig)	Yes	С
nfloresc.	Extension from leaf sheath (le)	Yes	D (1-4)
	Length of visible peduncle (Ipd)	Yes	C
	No. of visible branches in lowest whorl (Ilb)	No	C
	Height from lowest whorl (Ih)	Yes	C
	Width (Iw)	Yes	C
	Height to width ratio (Ih:Iw)	No	C
	Stiffness (Ia)	Yes	D (1-4)
	Pedicel colour (Ipc)	No	D (1-5)
	Spikelet clustering (Sa)	Yes	D (1-3)
Spikelet	Outer glume colour (Sc)	No	D (1-5)
	Glume gape (Sg)	Yes	D (1-4)
Lower glume	Total length (Glt)	No	С
	Body length (Glb)	Yes	C
	Setae length (Gls)	Yes	C
	% setae of total length (Glsp)	No	C
Jpper glume	Total length (Gut)	No	 C
	Body length (Gub)	Yes	Ċ
	Setae length (Gus)	Yes	C
Both glumes	Scabridity of keels (K)	Yes	D (0-3)
	Ciliation of margins (M)	Yes	D (0-2)
	Total length ratio (Glt:Gut)	No	C (0 2)
emma	Total length (Lt)	No	С
	Body length (Lb)	Yes	C
	Setae length (Ls)	Yes	C
	% setae of total length (Lsp)	No	C
	Density of back hairs (B)	Yes	D (0-4)
	Coarseness of scabrid surface (Rc)	Yes	D (0-4)
	Density of scabrid surface (Rd)	Yes	D (0-3)
alea	Total length (Pt)	No	C
	Body length (Pb)	Yes	C
	Setae length (Ps)	Yes	C
	% setae of total length (Psp)	No	C

Appendix 1. Morphological plant characters measured and used in statistical analysis.

Rachilla extension	Total length incl. hairs (Re)	Yes	С
Awn	Total length (At)	No	С
	Column length (Ac)	Yes	С
	Bristle length (Ab)	Yes	C
	% bristle of total length (Abp)	No	С
	Awn attachment height from lemma base (Aa)	Yes	С
	% awn attachment of total length (Aap)	No	С
Anther	Total length (A)	Yes	С

* C = continuous variable, ** D = discrete variable [ordinal scales for discrete variables: Lr: 1= flat, 2 = flat and involute (as a result of drying out), 3 = flat and conduplicate (may become pseudo-convolute and/or slightly involute with age), 4 = conduplicate, 5 = convolute to strongly involute; le: 1 = not exserted or spreading, 2 = not exserted but spreading, 3 = not fully exserted but more or less fully spread, 4 = fully exserted; la: 1 = very stiff and erect, 2 = rather stiff and more or less erect, 3 = not stiff but erect to slightly drooping, 4 = lax and weeping; Ipc and Sc: 1 = light green, 2 = mid-green, 3 = greyish green (green with minute purple mottling), 4 = mid-purple, 5 = dark purple to reddish purple; Sa: 1 = spikelets overlapping and obscuring individuals, 2 = spikelets partly overlapping but individuals discernible, 3 = spikelets more or less separate witbout overlapping; Sg: 1= nil or scarcely gaping outer glumes, 2=slightly gaping outer glumes (up to 10°), 3 = moderately gaping outer glumes (10° to 30°), 4 = widely gaping outer glumes (> 30°); K: 0 = non scabrous, 1 = slightly scabrous, 2 = moderately scabrous, 3 = strongly scabrous (often with scaberulous sides as well); M: 0 = non ciliate, 1 =minutely or distantly ciliate, 2 = uniformly ciliate; B: 0 = non-hairy, 1 = occasional hairs only, 2 = slightly or distantly hairy, 3 = covered in bairs but surface still discernable, 4 = covered in hairs and surface obscured; Re: 0 =no bristles (but may be villous), 1 = minutely scaberulous, 2 = finely scaberulous, 3 = strongly scaberulous; Rd: 0 = not scaberulous (but villous), 1 = lightly scaberulous (generally scattered on central nerve of lemma and setae only), 2 = moderately scaberulous (generally upper lemma back, central nerve and setae only), 3 = densely scaberulous (upper lemma back, central nerve and setae to total lemma surface)].